1 Factors governing the assignment of visual consequence to the

2 corresponding action

3 Running title: Factors governing visuomotor binding

- Authors: Alexandra Reichenbach^{1,2,3}*, Buse M. Urgen^{1,4}, Sotirios Apostolakis¹, Liora Michlin¹, and Jörn
 Diedrichsen^{1,5}
- 7 Affiliations: ¹Institute of Cognitive Neuroscience, University College London, London, United Kingdom;
- 8 ²Faculty of Computer Science, Heilbronn University, Heilbronn, Germany; ³Center for Machine Learning,
- 9 Heilbronn University, Heilbronn, Germany; ⁴National Magnetic Resonance Research Center (UMRAM),
- 10 Bilkent University, Ankara, Turkey; ⁵The Brain and Mind Institute, University of Western Ontario,
- 11 London, Ontario, Canada
- 12 ORCID A. Reichenbach: 0000-0003-4199-3005; J. Diedrichsen: 0000-0003-0264-8532
- 13 *corresponding author:
- 14 <u>alexandra.reichenbach@hs-heilbronn.de</u>; Max-Planck-Str. 39, 74081 Heilbronn, Germany
- 15 AR designed the study, analyzed the data, wrote the manuscript and approved the final manuscript; BU
- 16 designed experiments 1 and 2, collected the data, analyzed the data and approved the final manuscript;
- 17 SA designed experiment 3, collected the data, analyzed the data and approved the final manuscript; LM
- 18 designed experiment 4, collected the data, analyzed the data and approved the final manuscript; JD
- 19 designed the study, wrote the manuscript and approved the final manuscript.
- 20 Conflict of interest: none

- 21 Funding: This work was funded by a postdoctoral fellowship of the Deutsche Forschungsgemeinschaft
- 22 (RE 3265/1-1) to A.R.

23 Abstract

24 To achieve fast feedback control of voluntary movements, the visual consequences of our motor 25 commands need to be quickly identified and analyzed by the motor control processes in the brain. These 26 processes work remarkably well even in complex visual environments and in the face of discrepancies 27 between physical actuator and visually perceived effect, e.g. when moving a computer mouse on a 28 visually crowded screen. Here we use an ambiguous situation in which a single cursor could be 29 controlled by either the left or the right hand to determine the visual and cognitive factors that 30 determine the assignment of a visual stimulus to the corresponding motor command. Our results 31 demonstrate that the visuomotor system is exquisitely sensitive to the spatio-temporal correlation 32 between cursor and hands, learning the appropriate mapping implicitly within several minutes. In 33 contrast, spatial proximity between end effector and visual consequence has an immediate but only 34 transient effect on the assignment process. Finally, an explicit instruction about which hand controls the 35 cursor only has a minor influence when the instruction is presented first. These findings provide insight 36 into the relative importance of the factors that determine the binding of visual information to the 37 corresponding motor structures to enable fast feedback control.

38

39

41 New & Noteworthy

- 42 For efficient visuomotor online control, the brain needs to solve the correspondence problem between
- 43 an ongoing movement and its visual consequences. Here we challenge the visuomotor system with an
- 44 ambiguous reaching task, in which the visual feedback was controlled by either hand or by a
- 45 combination of both. Our findings characterize the properties of a flexible assignment process that
- 46 quickly takes into account the spatio-temporal properties of movements and the visual scene.

47

48 Keywords

49 visuomotor control, visuomotor binding, automatic processing, vision for action

51 Introduction

52 Fast and accurate reaching movements rely heavily on visual information. Whether we want to shake 53 someone's hand or grasp a cup of coffee, the motor system utilizes visual feedback about both the hand 54 and the targets to improve the ongoing reach within 100ms (1-5). Under natural conditions, however, 55 re-afferent visual feedback about the hand and target is embedded into a complex visual scene, often 56 with many other objects present. Thus, one challenge for the nervous system is to extract the relevant 57 visual information and assign it to the corresponding motor control structures. While proprioception 58 may contribute to the disambiguation of re-afferent visual information (6), visual consequences of our 59 actions are also efficiently isolated when they do not match proprioception, e.g. when using a tool or 60 moving a computer mouse (7, 8). Reichenbach and colleagues (9) have suggested the existence of a privileged channel for re-afferent visual information regarding the controlled effector - termed 61 62 visuomotor binding. They demonstrated that this process can operate outside the focus of visual 63 attention and filters corresponding visual information from a cluttered scene more efficiently than it can 64 filter visual information about the target of the reach.

However, which factors determine whether a visual stimulus is used to control an ongoing motor command? We addressed this question by putting participants in an ambiguous situation, in which they moved both hands and observed a single cursor moving on the screen (10). To determine whether the visuomotor system assigned the cursor to the left or right hand, we displaced the cursor laterally during the movement, eliciting a fast and involuntary feedback correction (5). The strength of this correction on each hand was taken as a measure of visuomotor binding between cursor and that hand.

First, we investigated the influence of spatial proximity between visual and proprioceptive feedback. The
 binding of sensory stimuli of multiple modalities such as vision and touch (called multi-modal binding)
 depends strongly on spatial proximity between the two stimuli (11). Spatial distance and orientation has

also a large effect on deciding whether a moving stimulus is part of one's own or someone else's body
(6, 12-14). In contrast, when using a computer mouse, the movement occurs on a horizontal plane,
while the visual feedback is displayed on the vertical screen. Despite this discrepancy, feedback control
still works very fast and efficiently (7).

78 Second, we considered the importance of spatio-temporal correlation between motor commands and 79 visual feedback. This factor is clearly a very powerful determinant when inferring control or agency over 80 our environment (8, 15, 16), and is thought to be accomplished via a comparison of predicted and 81 observed visual consequences or our actions (17-20). In our experimental situation, the movement of 82 the cursor correlated highly with both the left and the right hand movement, given that the movement 83 of both hands were also highly correlated. In this situation, we were able to test whether the motor 84 system can even use small differences in these correlations to identify the hand that is actually in 85 control of the cursor.

Finally, we tested the effect of an explicit, cognitive instruction to associate the visual stimulus with one of the two hands. Although fast visual feedback corrections themselves are considered to be resistant against top down control (21, 22), a residual top down influence has been found when integrating actions and their visual effects in a perception task (23). Therefore, it is possible that cognitive control will also exert a modulatory influence on visuomotor binding.

91 Material and Methods

92 Participants

For the four experiments, we recruited 31 neurologically healthy right-handed volunteers from an
internal database (experiments 1 and 2: 10 participants, 24.7±4.0 years, 7 female; experiment 3: 10
participants, 24.9±3.7 years, 10 female; experiment 4: 11 participants, 26.2±4.8 years, 5 female). All
participants provided written informed consent prior to testing and were paid as compensation for their
time. They were naïve to the purpose of the experiments and debriefed after the experimental sessions.
The research ethics committee of University College London (London, United Kingdom) approved all
experimental and consenting procedures.

100 Apparatus and stimuli

101 Participants were seated comfortably in front of a virtual environment setup, leaning slightly forward 102 with their forehead supported by a forehead rest. They made 15cm reaching movements away from 103 their body while holding onto a robotic manipulandum (update rate 1kHz, recording of position and 104 force data at 200Hz) with each hand. Movements were performed involving shoulder, elbow, and wrist 105 movements in the horizontal plane at chest height. A mirror that was mounted horizontally above the 106 manipulanda prevented direct vision of the hands, but allowed participants to view a visual scene on an 107 LCD monitor (update rate 60Hz). The visual display was arranged such that stimuli appeared to be 108 exactly in the depth-plane on which the hands moved. The movements were instructed using two 109 starting boxes (unfilled white squares, 0.7cm size, 6cm to the left and right from body midline) and a 110 single target box (unfilled white square, 1cm size) on an otherwise black background. The hand positions 111 were represented by white discs (hand cursors, 0.5cm diameter) located vertically above the real 112 positions of the hands (Fig. 1). All visual stimuli were displayed with a time delay of 68±5ms.

113 General procedure

114 Participants started a trial by moving the hand cursors into the starting boxes, gently aided by a 115 pushback force. After 800ms, the two hand cursors were replaced by a single cursor and the target box 116 appeared 15cm straight above the starting boxes at the lateral position of the cursor. Participants were 117 informed that the movement of both hands contributed equally to the movement of the cursor 118 (experiments 1-3, for other instructions in experiment 4 see below) and were instructed to make fast 119 and accurate bi-manual reaching movements bringing the cursor into the target. The trial ended when 120 the hand velocity remained below 3.5 cm/s for 40ms. A trial was considered valid when reaching time 121 was shorter than 800ms and maximum velocity ranged between 50 and 80 cm/s. Valid trials with 122 endpoint accuracy of at least 7mm contributed a single point each for the overall score and were 123 rewarded with a visual target "explosion" and a pleasant tone. A running score was continuously 124 displayed above the targets. Feedback about invalid trials, successful reaches, and increase in score was 125 given via a color scheme at the end of each trial. More specifically, the target turned green for trials that 126 were rewarded with a point, red for trials with good timing parameters but insufficient accuracy, yellow 127 when the movement was too quick, and blue when the movement was too slow or lasted too long. 128 Participants were encouraged to use this visual feedback to adjust their movements on the following 129 trials if necessary.

The movement of the cursor was determined by a weighted average of the movements of the two hands: $velocity_{cursor} = w * velocity_{LH} + (1 - w) * velocity_{RH}$ with w=1 implying complete left hand control and w=0 complete right hand control. However, participants were instructed to move both hands forward, such that even when control was assigned to one hand only, the instantaneous velocity of both hands was highly correlated with the movement of the cursor. To assess the binding between the visual motion of the cursor and the motor control processes of each hand, we perturbed the visual cursor on randomly interspersed "perturbation" trials. The perturbation consisted of a 2cm displacement in lateral direction (defined as the x-direction) either to the left or to the right, and occurred once the average position of the two hands had moved 15% of the forward distance to the target (Fig. 1A). The perturbations could easily be detected and participants were informed about the occurrence of random perturbations before the experiment started. However, the responses to counteract such perturbations are highly automatic and hard to suppress (5).

142 In a subset of the trials, a "force channel" restricted the movements. The force data obtained with this 143 method is more sensitive for the detection of feedback responses than position data from free reaching 144 trials (5, 24). The sensitivity is in the same range as acceleration data with the advantage that the force 145 is measured directly and does not have to be derived by double differentiation of the position signal, 146 thus no additional noise is introduced. The force channel was implemented with a spring-like force of 147 7000 N/m applied in lateral direction, which guided the hands on a straight path to the targets. In these 148 trials, the cursor displacements were reversed 250ms after the initial displacement in order to enable 149 task success. In the perturbation trials without force channel the cursor displacement remained, such 150 that the participants needed to correct for the perturbations. The proportion of perturbation and force 151 channel trials were specific to each experiment.

Each experiment started with training blocks to familiarize participants with the setup and the task. The training blocks did not contain force channel trials in order to keep the decrease in force responses as low as possible throughout the experiment (5). Every experimental block lasted approximately 5 minutes and participants were encouraged to take breaks between blocks whenever they needed rest. An additional break of at least 5 minutes was enforced in the middle of each experimental session. We probed for the awareness about the experimental manipulations with a structured interview at the endof the respective experimental sessions.

159 **Experiment 1: Influence of spatial proximity**

160 Experiments 1 and 2 were performed by the same participants in two separate sessions, with the order161 of experiments counterbalanced across participants.

162 In experiment 1, the visual cursor was controlled by both hands equally (w=0.5), such that the 163 correlations between the two hands and the cursor were equal. We manipulated the spatial proximity 164 between the hands and their visual consequence by horizontally offsetting the visual cursor from the 165 midpoint between the two hands. The offset ranged from 8cm to the left (cursor position -8) to 8cm to 166 the right (cursor position 8) relative to the midline, in steps of 2cm, yielding 9 cursor positions (Fig. 1B). 167 Note that the actual hands were positioned at -6cm and 6cm, respectively. To enable straight reaching 168 movements, the horizontal target position was offset accordingly. Experiment 1 consisted of 12 blocks 169 with 54 trials each, one block containing fully randomized a full permutation of the experimental 170 conditions: 2* force channel (y/n) x 3* cursor displacement (left/right/none) x 9* target position (-8, -6, 171 ..., 6, 8 cm). The 1.5h session started with training blocks of 60 trials with cursor position 0 until 66% of 172 the reaches were valid (cf. General procedure). 95% of the experimental trials were valid, i.e. we could 173 average over 11.4 repetitions (range: 5 to 12 trials) for each of the 54 conditions for the analysis.

174 Experiment 2: Learning the spatio-temporal correlation

175 In experiment 2, the visual cursor was always located at midpoint between the two hands. Instead, we 176 manipulated the spatio-temporal correlation between each hand and the visual cursor by switching the 177 cursor control between left and right hand across blocks. This means that in a left hand control block 178 (w=1), the visual cursor followed the motion of the left hand, i.e. the correlation between left hand and 179 cursor was 1, and in a right hand control block (w=0) vice versa. Due to the tight coupling of the

180 movements of the hand, the cursor also had high correlations with the respective other hand. The 181 instruction stated that both hands are controlling the cursor to an equal amount. The experiment was 182 divided in 17 experimental "control blocks" of 60 trials each, with the first control block serving as baseline with equal hand control (w=0.5) and then the hand control switched between left and right 183 hands across control blocks with the starting order counterbalanced across participants. Every 5th trial 184 185 was a force channel trial with a pseudorandom cursor displacement to the left or right, i.e. each control 186 block comprised 6 perturbation trials to the left and 6 to the right. We refrained from perturbing trials 187 without a force channel since the corrective movement might provide additional information about the 188 spatio-temporal correlation. We also skipped force channel trials without perturbation because force 189 channel trials prevent movement in the lateral direction and therefore break the spatio-temporal 190 correspondence between intended movement and visual feedback, which we wanted to keep to a 191 minimum. The remaining trials were therefore unperturbed, unconstrained reaching movements. In 192 order to mask the transition between control conditions, the experiment was divided into 15 physical 193 blocks of 68 trials each, i.e. the breaks between physical blocks did not correspond to the condition 194 switches. The 2h session started with training blocks of 60 trials with cursor position 0 and equal hand 195 control until 66% of the reaches were valid (cf. General procedure). From the 15 experimental blocks, 196 94% of the perturbation trials were valid, i.e. we could average over 45.1 repetitions (range: 36 to 50 197 trials) for each of the 4 conditions (2 control conditions (left/right) x 2 perturbations (left/right)) for the 198 analysis. To examine the development of the feedback responses within a control condition, we 199 analyzed the experimental control blocks by dividing them into an early, middle, and late phase, each 200 comprising 20 trials, and then averaged across control blocks. For each phase, we could then average 201 over 13.4 perturbation trials for each of the 12 conditions (2 control conditions (left/right) x 2 202 perturbations (left/right) x 3 phases (trials 1-20/trials 21-40/trials 41-60)).

203 Experiment 3: Interaction between spatial proximity and spatio-temporal correlation 204 After testing spatial proximity and spatio-temporal correlation individually, we aimed at investigating 205 their interaction over time in order to learn whether the two factors might be processed individually or 206 integrated into a common mechanism. To this end, we combined 5 cursor positions with 5 cursor 207 control conditions. The visual cursor was either displayed in the middle between both hands (position 208 0), directly above the left or right hand (positions -6 / 6), or between each hand and the midpoint 209 (positions -3/3). The control over the cursor was either shared equally between hands (w=0.5), fully 210 based on left (w=1) or right (w=0) hand movements, or shared in a 1:3 ratio between hands (w=0.25 or 211 w=0.75). Participants were instructed as in experiments 1 and 2. We prevented them from determining 212 the control of the cursor by only moving one arm by only displaying the visual cursor when both 213 manipulanda moved simultaneously. Each of the 25 experimental position/control conditions was tested 214 in two consecutive physical blocks consisting of 62 trials each in a randomised sequence across 215 participants. We introduced a washout block of 32 trials between two experimental position/control 216 conditions, in which the cursor was presented at position 0 and the visual cursor was controlled equally 217 by both hands (w=0.5). These aimed at removing putative learning effects of the preceding condition. 218 The first two trials of each experimental block were unperturbed, unconstrained reaches to introduce 219 the position/control condition. The remaining block consisted of 12 repetitions of the trial type 220 conditions (2 force channels $(y/n) \times 2$ cursor displacements (left/right), plus one unperturbed trial 221 without force channel). The experiment was completed in four sessions of 1.5h each. In the beginning of 222 the first session, participants performed training blocks structurally identical to the washout blocks until 223 75% of the reaches were valid (cf. General procedure). In total, each participant executed 74 physical 224 blocks after training: 2 times 25 experimental blocks and 24 interleaved washout blocks. Similar to 225 experiment 2, we divided each physical block, after cutting the leading 2 trials, into an early, middle, and 226 late phase, each comprising 20 trials for the analysis, leading to 6 phases for each position/control

227 condition. 95% of the experimental perturbed force channel trials were valid, i.e. we could average over

3.8 repetitions (range: 1 to 4 trials) per phase (trials 1-20/trials 21-40/trials 41-60/trials 61-80/trials 81-

229 100/trials 101-120) and condition (5 position (-6, -3, 0, 3, 6 cm) x 5 control conditions (w=0, 0.25, 0.5,

230 0.75, 1) x 2 channel conditions (y/n) x 2 perturbations (left/right)) for the analysis.

231 Experiment 4: Interaction between spatio-temporal correlation and cognition

232 To test for a cognitive modulation onto the feedback responses, participants were instructed on a block-233 by-block basis that their left, right, or both hands were in control of the visual cursor. This instruction 234 was additionally displayed below the starting positions throughout the experiment (Fig. 1C). In order to 235 have them moving both hands, the additional instruction was that both hands had to reach a target 236 zone, which was displayed 24cm around the target in horizontal direction. Furthermore, we only 237 displayed the visual cursor if both manipulanda were moved. The order of the three control instructions 238 was counterbalanced across participants and this order was kept constant for the duration of the 239 experiment across the 9 experimental conditions, i.e. the order of the three instructions was repeated 240 three times for each participant. The actual control over the cursor (w=0, 0.5, or 1) was randomized 241 within participants irrespective of the instructions given and all participants were tested on every 242 condition. Each of the 9 experimental instruction/control conditions was tested in two consecutive 243 physical blocks, each consisting of 62 trials in a pseudo-randomised sequence across participants, similar 244 to experiment 3. Again we had a washout block of 32 trials between two experimental 245 instruction/control conditions, in which the visual cursor was controlled equally by both hands with 246 matched instruction. These aimed at removing putative learning effects of the preceding condition. The 247 first two trials of each experimental block were unperturbed, unconstrained reaches to introduce the 248 instruction/control condition. The remaining block consisted of 12 repetitions of the trial type conditions 249 (force channel $(y/n) \times cursor$ displacement (left/right), plus one unperturbed trial without force 250 channel). In the beginning of the 2h session, participants performed training blocks structurally identical

251 to the washout blocks until 75% of the reaches were valid (cf. General procedure). In total, each 252 participant executed 26 physical blocks after training: two times 9 experimental blocks and 8 interleaved 253 washout blocks. After the structured interview at the end of the experiment, the participants were 254 additionally asked to rate, on a scale of 0 (not at all) to 5 (very well), how well they could control the 255 cursor for each of the instruction conditions. They were then debriefed and asked to guess the actual 256 control condition in the last block that they completed. As in experiment 3, we divided each physical 257 block, after cutting the leading 2 trials, into an early, middle, and late phase, each comprising 20 trials 258 for the analysis, leading to 6 phases for each instruction/control condition. 92% of the executed probe 259 trials were valid, i.e. we could average over 3.7 repetitions (range: 1 to 4 trials) per phase (trials 1-260 20/trials 21-40/trials 41-60/trials 61-80/trials 81-100/trials 101-120) and condition (3 instructions (left/both/right) x 3 control conditions (w=0, 0.5, 1) x 2 channel conditions (y/n) x 2 perturbations 261 262 (left/right)) for analysis.

263 Data analysis

Trials were excluded as invalid from further analysis when they did not meet the movement time (< 800ms) or speed (50-80 cm/s) criteria. Movement start and end time-points were defined as the velocity exceeding or falling below 2.5 cm/s for at least 40ms. All position and force traces were aligned temporally to the onset of the visual perturbations, or the point in time when the perturbation would have occurred for unperturbed trials. For all analyses, we took into account the delay of the visual display, which was measured empirically with a photodiode (68±5 ms).

To assess the size of the corrective responses, we measured the lateral forces exerted into channels (perpendicular to the reaching direction, Figs. 1A-C and 2A&B). A measure of correction strength for each hand was obtained by taking the difference between the force correcting for leftward displacements and the force correcting for rightward displacements. This subtraction automatically

removed any constant forces in the channel that were caused by the biomechanical properties of the
arm and robot. To obtain a time-averaged single measure for each hand and correction type, we
averaged the force difference in the time interval from 180 to 280 ms after perturbation onset
(*CorrectionStrength*). For assessing the relative response strength for the hands, we constructed an *AsymmetryIndex* based on the *CorrectionStrength* such that responses only with the right hand
correspond to *AsymmetryIndex*=0 and responses only with the left hand correspond to *AsymmetryIndex*=1:

$AsymmetryIndex = \frac{CorrectionStrength_{LH}}{CorrectionStrength_{LH} + CorrectionStrength_{RH}}$

The onset asynchrony between hands was defined as the difference between the movement onsets of the two hands for free reaching trials only. The correlation between hands (for combined x and y velocity) was based on the free reaching trials without displacements.

The linear regression models to test for the influence of different factors on the variance of the data were all validated with a leave-one-condition out cross validation approach. The reported R² values therefore do not constitute the proportion of variance explained, but the amount of variance predicted.

287 Whenever the goal of the analysis was to confirm hypotheses based on the results of previous studies,

we computed one-tailed *t*-tests according to these hypotheses. For demonstrating novel effects or

interactions, we computed two-tailed *t*-tests or repeated measures ANOVAs. Corrections for multiple

290 comparisons were performed using Bonferroni corrections where necessary. *P* values smaller than .05

are reported as significant. All values reported are mean values across participants with their respective

standard errors of the mean (SEM) unless stated otherwise. Effect sizes were calculated with Cohen's d

for correlated measures.

295 **Results**

296 **Position has an instantaneous modulatory effect on visuomotor binding**

297 All participants showed with both hands rapid movement corrections counteracting the cursor 298 displacements, with the position of the cursor modulating the relative response strength of each hand 299 (Fig. 2). When the cursor was displayed on the leftmost position, the left hand responded stronger than 300 the right hand (Fig. 2A) and vice versa for the cursor on the rightmost position (Fig. 2C). For visual cursor 301 positions at the midpoint between both hands, the left hand responded slightly stronger (Fig. 2B) (10, 302 25). The cursor position did not change the overall *CorrectionStrength* (see data analysis) averaged over 303 the hands (Fig. 2D, cursor position $F_{8,72}$ = 1.327; p = .244). However, there was a significant hand x cursor 304 position interaction ($F_{8,72}$ = 5.638; p < .001). Specifically, the closer the visual cursor was to each hand, 305 the stronger the hand responded. The same observation can be seen in the effect of the cursor position 306 on the AsymmetryIndex (Fig. 2E; $F_{8,72}$ = 4.807; p < .001) with a large effect size on the difference between 307 the two most outward cursor positions (d = 0.797).

308 Finding differential effects of cursor position on the feedback assignment of each hand raises the 309 question whether this influence is immediate or whether the history of past trials also affects the 310 movement correction. To test for a carry-over effect from the previous trial, we compared two linear regression models: One, which only uses the position of the current trial as an explanatory variable, one 311 312 that uses the positions of the current and previous trials. The former predicted 70.3±5.5% of the variance in the AsymmetryIndex (cross-validated) whereas the latter did not have an additional 313 314 predictive effect (69.8±5.5%). Taken together, the results demonstrate the spatial proximity between 315 the moving effector and the visual consequences affects the distribution of feedback correction in an 316 immediate fashion and does not produce lingering effects on the next movement.

317 Small differences in correlation influence learning over a short time frame

318 In experiment 2, we tested how small differences in spatio-temporal correlation between visual cursor 319 and hand movements influence visuomotor binding. In separate experimental control blocks of 60 trials 320 each, we switched the control over the cursor between hands such that the correlation for the hand in 321 control was 1. However, participants had to move both hands in parallel, which yields strong 322 synchronization of the two hands (26, 27). The average onset asynchrony between hands was 323 5.99±3.16ms with a within-subject standard deviation of 14.26±1.64ms. For x- and y-direction combined 324 the average correlation of the hand not in control and the cursor was $r = .85\pm.02$ (range: .75 to .97) 325 without differences between left and right hand control ($t_9 = 0.325$; p = .753). 326 Although the cursor was correlated only slightly more with the hand that was in control, than with the 327 other hand, this small difference strongly influenced the response strength of the two hands (Fig. 3A&B). 328 More specifically, blocks in which the cursor was controlled by the left hand (Fig. 3A) yielded a 329 significant higher AsymmetryIndex ($t_9 = 4.638$; p = .001; two-tailed; d = 1.154) than blocks in which the 330 cursor was controlled by the right hand (Fig. 3B). Dividing each block in an early (trials 1-20), middle 331 (trials 21-40), and late phase (trials 41-60) and averaging over all blocks of each control condition 332 revealed a consistent decrease in response strength for the hand not controlling the cursor (Fig. 3C&D; 333 interaction phase x control x hand: $F_{2,18}$ = 5.100; p = .018). More specifically, the right hand 334 *CorrectionStrength* decreased significantly from the early to the late phase in the left hand control 335 condition (Fig. 3C; t_9 = 3.505; p = .007; two-tailed), and the left hand *CorrectionStrength* decreased 336 significantly from the early to the late phase in the right hand control condition (Fig. 3D; t_9 = 3.046; p = 337 .014; two-tailed). The corresponding asymmetry indices confirm the shift of visuomotor binding within a 338 block (Fig. 3E; interaction phase x control: $F_{2,18}$ = 6.753; p = .007). The control effect on the asymmetry 339 index was not yet significant for the first 20 trials (early phase; $t_9 = 2.037$; p = .036; one-tailed; before

340 correction for multiple comparisons), but remained robustly significant thereafter ($t_g > 4.666$; p <= .002; 341 one-tailed; Bonferroni-corrected).

These results demonstrate that visuomotor binding can detect small differences in the spatio-temporal correlation between different motor commands and the putative visual consequence, and adjusts the response gains of the hands after a few reaches.

345 Influence of position and spatio-temporal correlation over time

The previous two experiments demonstrated that both spatial position of the cursor and spatiotemporal correlation between cursor and hand movements influence visuomotor binding. In the 3rd experiment we asked how these two factors interact over the time course of a block, in which the motor system could learn to associate the cursor movement with one of the hands. We therefore conducted an experiment in which both factors were varied together with 5 levels of cursor position x 5 levels of cursor control in a block design.

As can be seen from the average asymmetry indices (Fig. 4A-C), both factors had a distinct influence on 352 353 the response pattern at different time points within the course of each condition. The early phase (trials 354 1-20) is primarily driven by the cursor position (Fig. 4A), while the late phase of the second block (trials 355 101-120) is heavily driven by the control (Fig. 4C). Examining the two factors individually confirmed for 356 control (Fig. 4D) the results from experiment 2: The AsymmetryIndex scaled with the actual control over 357 the cursor (main effect control: $F_{4,36}$ = 18.585; p < .001), and this modulation changed over time 358 (interaction phase x control: $F_{20,180}$ = 5.404; p < .001). Specifically, the AsymmetryIndex significantly 359 increased for the left hand control conditions and significantly decreased for the right hand control 360 conditions from the early phase of the first block (trials 1-20) to the late phase of the second block (trials 361 101-120) (Fig. 4D; all p < .05). The influence of cursor position, however, was already very pronounced in 362 the beginning and stayed rather stable across the course of the blocks (Fig. 4E; main effect cursor

position: $F_{4,36}$ = 19.037; p < .001). Even though we found a significant interaction between phase and cursor position ($F_{20,180}$ = 2.123; p = .005), the influence of cursor position had a tendency to decrease rather than to increase over time.

366 To further quantify the contribution of each factor to the response pattern and test for interactions, we 367 estimated two linear regression models. Both models comprised an intercept and the factors cursor 368 position and control for explaining the AsymmetryIndex, and the second model additionally featured the 369 interaction between the two factors. The pure additive model predicted already 91.6±1.5% of the 370 variance in the AsymmetryIndex data (cross-validated), independent of the phase within the block (main 371 effect phase: $F_{5,45} = 0.991$; p = .434). Both factors contributed significantly in all phases except for control 372 in the first phase (Fig. 4F; all regression weights > 0: p < .05; two-tailed; Bonferroni-corrected). Their 373 relative contribution, however, changed significantly over time (interaction phase x factor 374 (position/control): $F_{5,45}$ = 10.834; p < .001). Specifically, the control factor significantly increased from 375 the early phase of the first block (trials 1-20) to the late phase of the second block (trials 101-120) (Fig. 4F). The constant intercept of 0.602±0.035 was significantly above 0.5 (t_9 = 2.949; p = 0.016), which 376 377 indicates analogue to the results from experiment 1 a general left-hand bias in responsiveness (10, 25). 378 Including an interaction term in the regression model neither increased the predicted variance 379 $(91.0\pm1.6\%)$, nor did the regression weights of the interaction term contribute in any phase (all p > .05; 380 uncorrected).

Taken together, these results suggest an independent influence of spatial proximity between effector and visual consequence and spatio-temporal correlation between motor commands and visual consequence. The importance of these two factors, however, changed over time: Spatial proximity had an immediate and sustained effect over visuomotor binding while the spatio-temporal correlation was learned within the short time frame of 124 movements.

386 Implicit assignment processes dominate over explicit instructions

387 Finally, in experiment 4, we asked to what degree visuomotor binding would be influenced by explicit 388 knowledge about which hand controls the cursor. We instructed participants that either the left, the 389 right, or both hands were in control over the cursor, and then varied the actual control independently in 390 a 3x3 design. The effect of the actual control (Fig. 5A) confirms the results from experiments 2 and 3: 391 The AsymmetryIndex was influenced by which hand had control over the cursor (main effect control: $F_{2,20}$ = 25.819; p < .001), and this modulation increased over time (interaction phase x control: $F_{10,100}$ = 392 393 6.209; p < .001). Specifically, the AsymmetryIndex significantly increased for left hand control and 394 significantly decreased for right hand control from the early phase of the first block (trials 1-20) to the 395 late phase of the second block (trials 101-120) (Fig. 5A; all p < .01). 396 In contrast, the influence of the explicit instruction was relatively weak in the beginning and then decreased over time (Fig. 5B; main effect instruction: $F_{2,20} = 5.708$; p = .011; interaction phase x 397 instruction: $F_{10,100} = 1.845$; p = .062). To determine to what degree participants were aware that the true 398 399 control of the cursor differed from the explicit instructions, we conducted a structured interview at the 400 end of the experiment. We found that only 2 participants reported that "the instruction seemed to be 401 mixed up for some blocks" when they were queried whether they noticed anything. This subjective 402 assessment was corroborated by the final forced-choice question after de-briefing, in which participants 403 had to indicate which hand they believed to have controlled the cursor in the last block. Only 4 out of 11 404 participants (36.4%) guessed the last block correctly, very close to the 33% chance level. Thus, the vast 405 majority of our participants was not aware of the control manipulation. It is therefore unlikely that the 406 gradual increase of the importance of control and the decrease of the importance of explicit instruction 407 was due to a conscious shift in strategy, but likely reflected a more implicit learning process.

Taken together, these results demonstrate that top-down control exerts only a marginal influence over visuomotor binding, which seems to be mostly dictated by the spatio-temporal correlation between movement and visual consequence. Furthermore, the congruency, or incongruency, between motor commands and visual stimulus can be subtle enough to bypass conscious awareness, but still strong enough to influence fast feedback control. Note that the instruction was clearly visible on the screen throughout the entire experiment, and still it had no more influence on visuomotor binding once the nervous system got used to the current environment.

416 **Discussion**

417 The current study sets out to investigate the factors that determine whether a visual stimulus is 418 attributed to one's own actions and therewith processed via the privileged channel of visuomotor 419 binding (9). We confronted the visuomotor system with an ambiguous situation in which a visual 420 stimulus could be attributed to the motor command of either hand (10). Our results demonstrate that 421 three factors influenced which hand the cursor control was assigned to. Specifically, spatial proximity 422 between visual and proprioceptive hand positions immediately biased the binding mechanism towards 423 the closer hand on a trial-by-trial basis. Small differences in the spatio-temporal correlation between 424 motor commands and visual consequence exerted an influence, which built up over the time course of 425 only few minutes and acted additively to the influence of spatial proximity. Explicit instructions, 426 however, exhibited only a negligible initial influence that vanished quickly. 427 A flexible coupling between visual and proprioceptive re-afferent signals benefits situations where the 428 task relevant visual consequences do not match hand positions. Skilled tool use would indeed be 429 impossible if only the visual re-afferences corresponding exactly to our hand positions were 430 incorporated into the body scheme (28, 29). The significant impact of spatial proximity in our experiments, however, provides a further demonstration of the importance of proprioception for visual 431 432 processing of our own moving body (6, 12-14). Furthermore, the short-term influence of this factor 433 suggests that proprioceptive re-afferences serve as an instantaneous bias for disambiguating the 434 situation. 435 Spatio-temporal correlations are a very influential factor for biasing visuomotor binding towards one 436 hand or the other (8). Even though the difference in the correlation between hands and cursor was 437 rather small and was not easily consciously detected, we observed in three independent experiments

that this correlation difference was enough for the motor system to determine which hand controlled

the cursor. The fact that participants were unaware of the manipulation, however, illustrates the
subtlety of this factor and provides a further example for efficient visuomotor processes that escape
conscious perception. Whether the perceived cursor movement is matched to prediction based on the
efferent motor commands, or directly to the re-afferent proprioceptive input from the arm cannot be
disentangled with this study. Based on the inaccuracy of proprioception (2, 30, 31), a role of the efferent
signals is very likely.

445 A larger relative binding of one hand to the visual cursor could be achieved by an up-regulation of the 446 control gains of the corresponding hand, the down-regulation of the other hand, or a combination of the 447 two. If the motor system assigned the control to the two hands in a competitive manner, we would have 448 expected the latter situation. In our experiments, however, we found that the strength of the feedback 449 response of the hand in charge remained constant while the feedback response of the other hand 450 decreased (cf. Fig. 3C&D). This suggests that the binding mechanisms of both hands are to some degree 451 determined independently. Interestingly, the down-regulation never reached a state where one hand 452 stopped to respond completely. However, the experimental blocks were rather short and it might be 453 that – given enough time – the learning process could complete such that one hand ceases completely 454 to respond.

While our experiments provide some insight into the temporal evolution of learning the binding between actions and their visual consequences, some questions remain open. We see a small, albeit non-significant effect already for the first 20 trials of a new control condition (cf. experiment 2). How quickly this adjustment in response to a change in visuo-spatial correlation occurs, is yet to be determined. Interestingly, we also observe a small relapse towards the baseline between two consecutive blocks of the same condition, which was negligible in experiment 4 (cf. Fig. 5A), but relatively clear in experiment 3 (cf. Fig. 4D&F). This suggests that, at least in ambiguous situations like

the one tested, there might be a prior towards a shared assignment. This prior seems to be rather strongand determines the binding for the first movements.

Whether the spatio-temporal correlation between an effector and its visual consequence or their spatial proximity is more important cannot be conclusively answered with our findings. The immediate effect of spatial proximity demonstrate the advantage of this factor. On the long run, however, the spatiotemporal correlation seems to become more important. This is indicated by the larger effect size of the experimental manipulation of experiment 2 compared to experiment 1 and in the regression weights of experiment 3 (Fig. 4F, see also Fig. 4C). Our experiments were not designed though to pit the two factors against each other.

471 Our last experiment clearly demonstrates that the cognitive influence over visuomotor binding is 472 negligible. Even though the instructions were clearly displayed throughout the whole course of the 473 experiment, we found that their initial small influence quickly decreased and finally vanished. The 474 answers to the final forced-choice question after this experiment demonstrate the subtlety of the 475 control manipulation and render the possibility that the findings in experiments 2 to 4 were driven by a 476 cognitive strategy unlikely. If participants believed the instructions, and the free report in the de-briefing 477 suggests so, then a voluntary up-regulation of the instructed hand would have been benefitted task 478 success. However, such behavior was not reflected in the movement data. In contrast, it seemed that 479 the visuomotor system relied on bottom-up correspondence of visual observation and motor commands 480 rather than accepting a top-down prior. This demonstrates again the differences of the visuomotor 481 system to perceptual processes, where top down influence can only weaken but not abolish the 482 integration between an action and its visual consequence (23).

The attribution of a visual percept to one's own action is widely investigated under the umbrella term
"agency" from different perspectives in various disciplines such as neuroscience, philosophy,

485 psychology, and psychiatry. In contrast to visuomotor binding, agency is almost exclusively defined on 486 the conscious perception level, and mostly investigated in distinction between other person's and one's 487 own actions. Here, we demonstrate that the motor system is exquisitely sensitive to relation of visual 488 consequences and own actions, even if this escapes conscious awareness. Utilizing ambiguous 489 visuomotor tasks as in the present study allows future research to find communalities and differences 490 between aware and unaware processes attributing visual stimuli to one's own actions. This adds to the 491 repertoire of experimental paradigms with the possibility not only to dissociate one's own from 492 someone else's action but on a fine grained level the assignment within a person.

Our findings might further inform the design of tools or user interfaces where rapid processing of its visual feedback is essential. Examples here are advanced prosthesis, tele-operation systems, or other devices where the physical movement is detached from its visual consequence. Our results suggest that spatio-temporal correlation is of utmost importance for establishing effective feedback control. The design of these systems therefore should focus on delivering veridical visual feedback to the physical movement. If this is given, the human visuomotor system will be able to use these devices intuitively.

499

501 **References**

502 Pelisson D, Prablanc C, Goodale MA, and Jeannerod M. Visual control of reaching movements 1. 503 without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the 504 hand to the final position of a double-step stimulus. *Exp Brain Res* 62: 303-311, 1986. 505 2. Sarlegna F, Blouin J, Bresciani JP, Bourdin C, Vercher JL, and Gauthier GM. Target and hand 506 position information in the online control of goal-directed arm movements. Exp Brain Res 151: 524-535, 507 2003. 508 3. Saunders JA, and Knill DC. Humans use continuous visual feedback from the hand to control fast 509 reaching movements. Exp Brain Res 152: 341-352, 2003. 510 Saunders JA, and Knill DC. Visual feedback control of hand movements. J Neurosci 24: 3223-4. 511 3234, 2004. 512 5. Franklin DW, and Wolpert DM. Specificity of reflex adaptation for task-relevant variability. J 513 Neurosci 28: 14165-14175. 2008. 514 6. Viswanathan S, Fritz C, and Grafton ST. Telling the right hand from the left hand: multisensory 515 integration, not motor imagery, solves the problem. *Psychol Sci* 23: 598-607, 2012. 516 7. Brenner E, and Smeets JB. Fast corrections of movements with a computer mouse. Spat Vis 16: 517 365-376, 2003. 518 Debats NB, Ernst MO, and Heuer H. Kinematic cross-correlation induces sensory integration 8. 519 across separate objects. Eur J Neurosci 46: 2826-2834, 2017. 520 9. Reichenbach A, Franklin DW, Zatka-Haas P, and Diedrichsen J. A dedicated binding mechanism 521 for the visual control of movement. Curr Biol 24: 780-785, 2014. 522 White O, and Diedrichsen J. Responsibility Assignment in Redundant Systems. Curr Biol 2010. 10. 523 11. Gepshtein S, Burge J, Ernst MO, and Banks MS. The combination of vision and touch depends 524 on spatial proximity. J Vis 5: 1013-1023, 2005. 525 12. Krugwasser AR, Harel EV, and Salomon R. The boundaries of the self: The sense of agency 526 across different sensorimotor aspects. J Vis 19: 14, 2019. 527 Kannape OA, Schwabe L, Tadi T, and Blanke O. The limits of agency in walking humans. 13. 528 Neuropsychologia 48: 1628-1636, 2010. 529 van den Bos E, and Jeannerod M. Sense of body and sense of action both contribute to self-14. 530 recognition. Cognition 85: 177-187, 2002. 531 Haggard P, and Tsakiris M. The Experience of Agency: Feelings, Judgments, and Responsibility. 15. 532 *Curr Dir Psychol Sci* 18: 242-246, 2009. 533 16. Moore JW, and Fletcher PC. Sense of agency in health and disease: a review of cue integration 534 approaches. Conscious Cogn 21: 59-68, 2012. 535 17. Fletcher PC, and Frith CD. Perceiving is believing: a Bayesian approach to explaining the positive 536 symptoms of schizophrenia. Nature Reviews Neuroscience 10: 48-58, 2009. 537 Lindner A, Thier P, Kircher TTJ, Haarmeier T, and Leube DT. Disorders of agency in 18. 538 schizophrenia correlate with an inability to compensate for the sensory consequences of actions. 539 Current Biology 15: 1119-1124, 2005. 540 19. Synofzik M, Vosgerau G, and Newen A. Beyond the comparator model: A multifactorial two-541 step account of agency. *Consciousness and Cognition* 17: 219-239, 2008. 542 Voss M, Moore J, Hauser M, Gallinat J, Heinz A, and Haggard P. Altered awareness of action in 20. 543 schizophrenia: a specific deficit in predicting action consequences. Brain 133: 3104-3112, 2010. 544 Day BL, and Lyon IN. Voluntary modification of automatic arm movements evoked by motion of 21. 545 a visual target. Exp Brain Res 130: 159-168, 2000.

- 546 22. Pisella L, Grea H, Tilikete C, Vighetto A, Desmurget M, Rode G, Boisson D, and Rossetti Y. An
- 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nat Neurosci* 3: 729-736, 2000.
- 549 23. **Debats NB, and Heuer H**. Explicit knowledge of sensory non-redundancy can reduce the 550 strength of multisensory integration. *Psychol Res* 84: 890-906, 2020.
- 551 24. Smith MA, Ghazizadeh A, and Shadmehr R. Interacting adaptive processes with different
- timescales underlie short-term motor learning. *PLoS Biol* 4: e179, 2006. **Reichenbach A, Costello A, Zatka-Haas P, and Diedrichsen J**. Mechanisms of responsibility
- assignment during redundant reaching movements. *J Neurophysiol* 109: 2021-2028, 2013.
- 555 26. **Diedrichsen J, Hazeltine E, Kennerley S, and Ivry RB**. Moving to directly cued locations abolishes 556 spatial interference during bimanual actions. *Psychol Sci* 12: 493-498, 2001.
- 557 27. **Kelso JA, Southard DL, and Goodman D**. On the coordination of two-handed movements. *J Exp* 558 *Psychol Hum Percept Perform* 5: 229-238, 1979.
- Johnson-Frey SH. The neural bases of complex tool use in humans. *Trends Cogn Sci* 8: 71-78,
 2004.
- 561 29. Takahashi C, Diedrichsen J, and Watt SJ. Integration of vision and haptics during tool use. *J Vis*562 9: 3 1-13, 2009.
- 56330.Rock I, and Victor J. Vision and Touch: An Experimentally Created Conflict between the Two564Senses. Science 143: 594-596, 1964.
- 565 31. **Ernst MO, and Banks MS**. Humans integrate visual and haptic information in a statistically 566 optimal fashion. *Nature* 415: 429-433, 2002.
- 567

569 Figure Captions

570 Figure 1

Experimental setup. A: Visual scene for all four experiments with additional setup information. A blend of hand and cursor positions at the start of a movement as well as 15% in the movement, the point in time when a cursor perturbation may occur, are depicted. B: Visual scene for experiment 1 with all possible spatial configurations. C: Visual scene for experiment 4 with the information about the control (here: left hand) and the target zone. Note that the grey elements, i.e. the manipulanda/hands and the target zone were not visible to the participants.

Effect of cursor position on corrective responses in experiment 1. Force traces (leftward – rightward displacements) for cursor position 8cm to the left (A), at the midpoint between both hands (B), and for cursor position 8cm to the right. Shaded areas denote 1 SEM. The dashed lines indicate the time window from 180 to 280ms, over which the forces are averaged to obtain the *CorrectionStrength* depicted in D. *CorrectionStrength* (D) and *AsymmetrIndex* (E) for all cursor positions. Error bars denote 1 SEM. Post-hoc test (two-tailed t-test): * p < .05. N=10 (7 female) in all panels and conditions.

584 Figure 3

585 Effect of cursor control on corrective responses in experiment 2. Force traces (leftward – rightward

586 displacements) for left hand controlling the cursor (A) and right hand controlling the cursor (B). Shaded

587 areas denote 1 SEM. The dashed vertical lines indicate the time window from 180 to 280ms, over which

the forces are averaged to obtain the *CorrectionStrength* depicted in C&D. Evolvement of

589 CorrectionStrength within a block for left hand cursor control (C), right hand cursor control (D), and the

corresponding *AsymmetryIndex* (E). Error bars denote 1 SEM. Post-hoc test (two-tailed t-test): * *p* < .05;
** *p* < .01. N=10 (7 female) in all panels and conditions.

592 Figure 4

593 Effects of cursor control and cursor position on corrective responses in experiment 3. Evolution of the 594 combined response pattern (AsymmetryIndex) to all 25 conditions over the course of two consecutive 595 blocks of each condition: early phase of the first block (A), late phase of the first block (B), late phase of 596 the second block (C). Each panel show a 2-dimensional representation of the mean AsymmetryIndex 597 (color-coded) as a function of the 5 positions (x-axis) and 5 control conditions (y-axis). The 598 representation of the AsymmetryIndex in a contour plot instead of a 5x5 grid was chosen to emphasize 599 the continuity of the two factors.. D: Marginals of control, averaged over all cursor position conditions; 600 E: Marginals of cursor position, averaged over all control conditions. F: Evolution of the regression 601 weights for each factor over the time of the two consecutive blocks of each condition. Error bars denote 602 1 SEM. The vertical dashed gray lines illustrate the break between physical blocks, in which the influence 603 of control significantly decreased (regression weight for control: $t_9 = 4.052$; p = .003; two-tailed t-test). 604 Post-hoc test (two-tailed t-test): * *p* < .05; ** *p* < .01; *** *p* < .001. N=10 (10 female) in all panels and 605 conditions.

606 Figure 5

Effects of cursor control and instruction on corrective responses in experiment 4. A: Marginals of control, averaged over all instructions; B: Marginals of instruction, averaged over all control conditions. Error bars denote 1 SEM. The vertical dashed gray lines illustrate the break between blocks, which had here very little influence on the regression weight for control (t_{10} = 0.341; p = .741; two-tailed t-test) Post-hoc test (two-tailed t-test): ** p < .01. N=11 (5 female) in all panels and conditions.











Factors governing the assignment of visual consequence to the corresponding action

